# THE EMBRYOLOGY OF *LYTTA VIRIDANA* LE CONTE (COLEOPTERA: MELOIDAE). IX. THE CENTRAL NERVOUS SYSTEM, STOMATOGASTRIC NERVOUS SYSTEM, AND ENDOCRINE SYSTEM [1].

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*The central nervous system of* Lytta viridana *arises in the usual way from ventral, longitudinal files of neuroblasts in the head, thorax, and first 10 abdominal segments of the embryo. Median nerve strand cells have two fates: clumped, intersegmental cells shift cephalad and differentiate into ganglion cells; intrasegmental cells probably develop into glial elements of the lateral nerve cords. The perilemma appears to originate from modified outer ganglion cells.*

*The stomatogastric nervous system develops from three evaginations in the roof of the stomodaeum: the frontal ganglion from the first, the hypocerebral ganglion and corpora cardiaca from the second, and the ventricular ganglion from the third. It is suggested that these three ganglia are not serially homologous with the intersegmental clumps of the post-oral median nerve strand.*

*A corpus allatum invaginates inward from the anterior face of each maxillary base and eventually fuses with a corpus cardiacum below the brain. Probable prothoracic glands proliferate inward between the interganglionic connectives from the ventral, labial-prothoracic intersegmental ectoderm. Their cells eventually spread over the surface of a transverse tracheal commissure emanating from branch 2 of the mesothoracic spiracular tracheal system.*

*Observations are discussed in relation to findings on the origin and function of comparable structures in other insects.*

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*Le système nerveu central de la* Lytta viridana *se forme d'une facon normale à partir de files ventrales et longitudinales de neuroblastes dans la tête, le thorax, et les dix premiers segments abdominaux de l'embryon. Les cellules nerveuses et étroites apparaissent en deux groups: les cellules intersegmentaires groupées s'assemblent antérieurement et se différencient en cellules ganglionaires et les cellules intrasegmentaires probablement se développent en éléments gliaux de la chaine nerveuse latérale. Le perilèmme semblent être formé de cellules ganglionaires externes et modifiées.*

*Le système nerveux stomatogastrique se développe à partir de trois evaginations dans la partie supérieure du stomodeum: du premier vient le ganglion frontal, du second le ganglion hypocérébral et les corpora cardiaca, et du troisième le ganglion ventriculaire. Nous suggérons que ces trois ganglions ne sont pas des homologues en série avec les groupes de cellules intersegmentaires du ruban nerveux median et post-oral.*

*Un corpus allatum pénètre à l'intérieur à partir de la face antérieure de la base de chaque maxillaire et éventuellement se fusionne avec un corpus cardiacum sous le cerveau. Les glandes prothoraciques probables prolifèrent vers l'intérieur entre les connectifs réunissant les ganglions subesophageaux et prothoraciques l'ectoderme intersegmentaire labial-prothoracique du côté ventral. Leurs cellules éventuellement se repandent au-dessus de la surface d'une commissure trachéaire transverse émanant de la branche 2 du système trachéaire et spiraculaire de mésothorax.*

*Les observations sont discutées en relation aux découvertes sur l'origine et la fonction de structures comparables chez d'autres insectes.*

## INTRODUCTION

Early stages in the embryonic development of blister beetles of the species *Lytta viridana* LeConte, have been described in previous papers in this series (Rempel and Church 1965, 1969 a, b, 1971; Church and Rempel 1971). Organogenesis and differentiation of individual organ systems are being treated in separate papers and the first of these, on the respiratory system, has already appeared (Rempel and Church 1972). This paper is devoted to the nervous and endocrine systems, to which brief reference has already been made (Rempel and Church 1969b; Church and Rempel 1971). Since Ullmann (1967) described development of the nervous system in *Tenebrio molitor* L. (Coleoptera, Tenebrionidae) in considerable detail, and because events in *L. viridana* are very similar, we here concentrate on aspects that supplement her publication.

Embryogenesis of the brain and lateral nerve cords of insects is well known (Edwards 1969; Anderson 1972 a, b, 1973) and quantitative analysis of the events involved has begun (Bate 1976; Kankel and Hall 1976). However, there is still controversy regarding the development and ultimate fate of the median cord or nerve strand. Although authors agree that the median cord arises from a continuous strip of median ectoderm between the lateral cords, few studies describe its development throughout embryogenesis.

Ontogeny of the stomatogastric nervous system has been thoroughly described recently for *T. molitor* by Ullmann (1967), for *Carausius (= Dixippus) morosus* Br. (Phasmatodea) by Scholl (1969), for *Oncopeltus fasciatus* Dallas (Heteroptera) by Dorn (1972, 1975 a, b) and for *Stenopsyche griseipennis* MacLachlan (Trichoptera) by Miyakawa (1974). Like earlier workers, these authors believed the system to develop from three evaginations in the roof of the stomodaeum. According to Ullmann (1967), the most anterior evagination gives rise to the frontal ganglion, the second to the hypocerebral ganglion, and the third to the ventricular ganglion. Scholl (1969) also followed development of the frontal ganglion back to the first evagination, but he considered the hypocerebral and ventricular ganglia to come from the third evagination and the corpora cardiaca from the second. Miyakawa (1974) claimed that the recurrent nerve arose from the second evagination. All three interpretations differ slightly from the traditional one of Roonwal (1937) where evagination 2 gives rise to the hypocerebral (occipital) ganglion and corpora cardiaca (pharyngeal ganglia).

Although many reviews are available about the structure and function of insect endocrine organs (e.g. Cazal 1948; Pflugfelder 1958; Herman 1967; Dorn 1972; Gilbert and King 1973; Sláma, *et al.* 1974; Novák 1975), their embryonic development has received little attention.

In this paper, we describe the embryogenesis of the central nervous system, stomatogastric

nervous system and endocrine system of *L. viridana*. Limited comment is made concerning the neuropile and neurosecretory cells since stains appropriate for these structures were not used. We have described all our methods in previous papers (Rempel and Church 1965, 1969b).

## OBSERVATIONS

### Central Nervous System

In *Lytta viridana*, segmentation precedes neurulation (Rempel and Church 1969b). The former process is initiated at approximately 36 h, with coelom formation being well advanced by 50 h. At this time, the ectoderm (ect), as seen in parasagittal section (Fig. 1), consists of a single layer of columnar cells with large nuclei and conspicuous vacuoles at their inner ends. In median sagittal section (Fig. 2), the cells appear to form an irregular double layer.

Neurulation begins at 56 h. The sequence of the two processes involved is similar to events in *T. molitor* embryos (Ullmann 1964, 1967) and is probably general in insect development. Many ectodermal cells (Fig. 3. nbl) enlarge in both their nuclei and cytoplasm and begin to stain more strongly than neighbouring cells. Gradually, they withdraw from the surface and move inward. As this process continues, the germ band soon separates into an outer dermatogene layer (dg. l) and an inner neurogene layer (ng: l). The latter consists of neuroblasts (nbl) which, by successive but unequal, vertical, teloblastic division, give rise to small pre-ganglion and ganglion cells (Fig. 4, ggl.c; see also Fig. 3 and 16 in Church and Rempel 1971). Pre-ganglion cells divide at least once, equally, and often at right angles to the neuroblasts, and generate ganglion cells. This process occurs in continuous, longitudinal files of cells extending on either side of the midline from the region of the stomodaeum to the proctodaeum.

Simultaneously, along the midline, cells in intrasegmental regions continue, by equal division, to form an apparent multi-layered strand of cells (m.n.c), while those in intersegmental regions develop into clumps of large, neuroblast-like, darkly-staining cells (Fig. 5, m.c.c; see also Fig. 17 and 18 in Church and Rempel 1971). At first, the dermatogene layer does not cover these clumps ventrally. These two classes of cells comprise the median nerve strand. This strand begins anteriorly in the intercalary segment (intc. seg) and extends posteriorly to a region behind the tenth lateral cord ganglia (Fig. 7, m.n.c). The first clump of cells is located in the intersegmental region between the mandibular and maxillary segments (Fig. 7, 11, 47), not, as was incorrectly stated earlier (Church and Rempel 1971, but see their Fig. 2), between the intercalary and mandibular segments.

Cephalic ganglia develop in the same way as do the lateral nerve cords. Large neuroblasts separate from the dermatogene layer, and, by repeated, unequal, teloblastic division, give rise to pre-ganglion and ganglion cells. The first pair of ganglia arise pre-orally and ultimately form the protocerebrum (Fig. 8, protc; as in *T. molitor* (Ullmann 1967) these ganglia are tri-lobed, the optic ganglia (op. l) arising as separate, ectodermal invaginations – (Fig. 42)); the second pair form paraorally and develop into the deutocerebrum (deutc) (Fig. 8); and the third pair arise postorally and later move into a pre-oral position to form the tritocerebrum (Fig. 9, 18, tritc). Simultaneously, the stomatogastric nervous system (stmg. n.s) arises from three evaginations in the roof of the stomodaeum (Fig. 10; in 1969, Rempel and Church, incorrectly referred to these as invaginations, as did Ullmann (1967) . Although they are *in*vaginations of the body wall, they are *ev*aginations of the stomodaeum). The cells surrounding the evaginations have large, light-staining nuclei and resemble neuroblasts of the central nervous system (Fig. 46). However, as Ullmann (1967) pointed out, they divide equally not teloblastically.

By 64 h, the lateral nerve cord ganglia have enlarged and have moved mesad. Meanwhile, the clumps of median nerve strand cells (m.c.c) have shifted cephalad from a strictly inter-

segmental position into an intrasegmental one in the preceding segment (Fig. 6, 39). Here, they later contribute to the posterior gangliomere of each ganglion.

By 88 h (see Fig. 1 in Rempel and Church 1971), neuroblasts are prominent in the protocerebrum which, by active division, produce columns of pre-ganglion and ganglion cells. The innermost of these, beginning at 72 h, have begun to grow out as axons (Fig. 12). Thus, by this time, a neuropile (npl; often called neuropil) is evident, both here and in all central nerve cord ganglia and connectives (Fig. 40). In each antenna, an ectodermal invagination has arisen which will eventually differentiate into an antennal sense organ (Fig. 12, ant. s.o). Its ontogeny will be the subject of a future contribution.

At 88 h, the tritocerebrum (tr. com) is still post oral and is still attached to the intercalary ectoderm (Fig. 11, 13, intc. seg). The mandibular (md. ggl), maxillary (mx. ggl) and labial ganglia (lb. ggl) have moved closer to each other, foreshadowing formation of the subesophageal ganglion (Fig. 11) but the 10 abdominal ganglia are still separate at this time. Cells of the median nerve strand clump (m.c.c) are still larger than their neighbours and their cytoplasm still stains more darkly (Fig. 11). They have become oval and have developed clearly discernible axons, which join in a bundle and extend forward and upward, reaching the dorsal region of the ganglion midway between the anterior and posterior cross commissures (Fig. 11, 47, com). These cells maintain this appearance until the end of embryogenesis, although not as obviously.

In cross sections through the tritocerebrum (Fig. 13), cells of the median strand differ little from those of ordinary, body wall ectoderm. In the mandibular region (Fig. 14), the strand appears as a cluster of cells having faintly stained nuclei. Sections through the posterior cross commissure (com), of the maxillary segment (Fig. 15) show numerous axonal extensions into the neuropile. Here, the median strand cells are small, rectangular and more lightly staining than neighbouring ganglion cells. Sections through the median nerve strand clump (m.c.c) of the labial ganglion (Fig. 16, 41) show its cells to be distinctly separate from those of the lateral cord ganglia. Finally, in the prothoracic-mesothoracic interganglionic region (Fig. 17), median strand cells are indistinguishable from those of ordinary, body wall ectoderm, suggesting that, at this time, the median strand has become discontinuous in intersegmental regions.

By 120 h (see Fig. 18 and 19 in Rempel and Church 1971), cephalization of the embryo has become more pronounced, and the head has become clearly set apart from the rest of the body. The gnathal ganglia have fused to form the subesophageal ganglion (Fig. 19, sb. ggl) and abdominal ganglia 9 and 10 have amalgamated (see Fig. 6 in Rempel and Church 1972). The lateral nerve cord ganglia have moved to the midline and have fused to form a single ganglionic mass in each segment. Ganglion cells have encroached ventrally upon the median strand, restricting it to the dorsal region of each ganglion (Fig. 20, 43, m.n.c). The strand seemingly has disappeared from intersegmental regions (Fig. 21) of the ventral nerve cord but it and its clumps (m.c.c) are retained in intrasegmental regions. For example, three clumps are clearly visible in the subesophageal ganglion. (Fig. 19).

A characteristic feature of this stage in development, is the presence of long, cytoplasmic strands (cyt. std) in the intersegmental regions, extending from the body wall (bd. w) to the interganglionic connectives (int. cn) and from there to the developing midgut (Fig. 21, mdgt). We do not know what significance they have and in embryos older than 132 h, they are no longer present.

By 132 h, a perilemma has appeared. It is best developed around the interganglionic connectives (Fig. 22) and consists of a layer of cells, the perineurium (prn), and its secretion product, the neural lamella (nr. lml; often termed neurilemma or neural lemma). Here and there, the interface between ganglion cells and neuropile (npl) is occupied by cells (gll. c) that have

small, light-colored nuclei (Fig. 20, 43). These cells first appear at about 104 h, and apparently originate from the median strand. We believe them to be glial. Springer (1967) and Springer and Rutschky (1969) referred to them as the inner sheath.

By 180 h, the entire central nervous system is enclosed by a well-developed perilemma. It is especially prominent about the interganglionic connectives (Fig. 25, 28, 56) and dorsally in each ganglion (Fig. 44). By this time, most neuroblasts have disappeared, although a few dividing in the brain remain active until hatching. The sheath of glial cells (gll.c) separating neuropile from ganglion cells within each ganglion is much more pronounced (Fig. 44) and a few small, dark-staining glial cells are scattered among ganglion cells throughout the central nervous system. Although inadequate staining makes their details impossible to sort out, fibre tracts and glomeruli are now clearly visible within the brain and ventral nerve cord ganglia. These first begin to take shape at 120 h (Fig. 43) and become steadily more complex until hatching at 250–264 h. (Fig. 44, 48).

Between 180 and 200 h, most changes affect the distribution of glial elements enclosing the neuropile (Fig. 23). The cells of the median strand clump (m.c.c) are still recognizable but can be confused easily with other ganglion cells. In parasagittal sections of the nerve cord (Fig. 24), the glial cells (gll. c) appear to be stacked up vertically at each end of each interganglionic connective, but transverse sections through these regions (Fig. 45) show they are not. In cross sections (Fig. 25-28) made at the points indicated by lines in Fig. 23 and 24, differences in distribution of glial cells can also be seen. In interganglionic connectives, the perineurium (prn) is thick dorsally and very thin ventrally, whereas the opposite is true of the neural lamella (nr. lml) (Fig. 24, 25, 28, 56). Except for continued differentiation of neuropile centres, no other significant changes were observed in nervous system development up to the time of hatching (250 to 264 h).

**Stomatogastric Nervous System (stmg. n.s.)**

In *Lytta viridana* embryos, when the stomodaeum begins to invaginate at 56 h, the three evaginations in its roof – the anlagen of the stomatogastric nervous system (stmg. n.s) – are already evident (see Fig. 50-53 in Rempel and Church 1969b). At 64 h (Fig. 10), nuclei of cells surrounding the evaginations become enlarged and, from 72 to 80 h (Fig. 11, 46), strands of cells arise behind each evagination and begin to stream forward over the roof of the stomodaeum. This movement is accompanied by considerable mitotic activity. By 96 h, the frontal ganglion (frt. ggl) has begun to enlarge and neuropile to differentiate within it (Fig. 47) (the latter actually commences at about 88 h). Simultaneously, fibres of the recurrent nerve (rct. nv) become apparent just behind the frontal ganglion. At 104 h (Fig. 29), forward streaming of nerve cells from the three stomodaeal evaginations is still evident but, by 120 h (Fig. 19), evaginations 1 and 2 have begun to disappear, and the three cell streams are no longer separable.

By 120 h, the frontal ganglion (frt. ggl) is well-developed (Fig. 19) and by 132 h, the hypocerebral ganglion (hyp. ggl) has appeared as a slight swelling in the recurrent nerve (rct. nv) below the pars intercerebralis (prs. intr) of the brain (Fig. 33). Evaginations 1 and 2 have disappeared and all cell proliferation now seems to arise from evagination 3 – an indication that this is a source of most cells comprising the recurrent nerve (rct. nv). The tritocerebral (= frontal) connectives of the frontal ganglion form at 120 h, (see Fig. 31, C, D in Rempel and Church 1971). By 156 h, the system is essentially complete, and from here on most changes involve ganglionic enlargement and an increase in length of the recurrent nerve to match continued growth of the stomodaeum. Fig. 38 shows the system as it appears at 216 h and Fig. 48 at 264 h.

**Endocrine System**

The endocrine system of *L. viridana* consists of neurosecretory cells, which we will not consider, and paired corpora cardiaca, corpora allata, and prothoracic glands.

The corpora cardiaca (crp. crd) first become recognizable at 96 h. They originate from cells emanating from evagination 2 in the roof of the stomodaeum, also the source of the hypocerebral ganglion (Fig. 29, 47). These cells move laterally around the stomodaeum (Fig. 31 c, 49) and, by 112 h, have been carried forward by the cell streams to the region of the pars intercerebralis (prs. intr). As this movement occurs, the cells comprising the cardiaca, become more and more loosely arranged (Fig. 50). Later, each gland rudiment shifts laterally and attaches to the posterior surface of the brain. By 132 h, the glands have established contact posteriorly with the corpora allata (crp. all) (Fig. 37). Differentiation of the glands' cells first becomes evident at about 120 h, both secretory(s) and glial elements being present (Fig. 50). The former resemble ganglion cells in their dark-staining, homogeneous, cytoplasm; the latter form a loose, parenchymatous network. By 250 h (Fig. 37, 51, 54), this network has contracted, so that the fully-formed glands are not much larger than the allata.

The corpora allata (crp. all) first become apparent at 56 h, as small, ectodermal invaginations of the anterior base of each maxilla (Fig. 34, 52). Each invagination grows inward and dorsad until, at 96 h (Fig. 53), it reaches a position below the caudal extension of the anterior tentorial arm (a. tent). It now shifts slightly laterally and then dorsally over the tentorial arm, maintaining, throughout this movement its connection with the body wall (Fig. 35, 36). At 112 h, this connection breaks.

In the meantime, the ventral tracheal trunk of each side (2 in Fig. 6 in Rempel and Church 1972) has extended forward from the mesothoracic spiracle over the posterior tentorial arm (p. tent). At 120 h, this trunk sends one branch (2b) to the gnathal appendages and another (2a) to the brain. The second branch becomes closely applied to the corpus cardiacum-corpus allatum complex (Fig. 13 and 17 in Rempel and Church 1972). At 120 h, each corpus allatum reaches its final position and, at 132 h, re-establishes its connection with the body wall via a clear, tendon-like strand (Fig. 37, 54). The connective tissue sheath of the corpus allatum, described by Weismann (1926) in *C. morosus* and by Roonwal (1937) in *L. migratoria*, was not evident in our preparations, even under oil immersion (Fig. 54).

At 96 h, two, small protuberances proliferate inward from the ventral, labial-prothoracic intersegmental ectoderm (Fig. 30, 55, pthr. gl). They originate close together and grow dorsad between the developing interganglionic connectives. (int. cn). At the same time, tracheae 2 (Fig. 6, 9 and 17 in Rempel and Church 1972) each give off a medially-directed branch (tracheae 9) to form a commissure above the ventral nerve cord between the subesophageal and prothoracic ganglia (Fig. 55, 56, trch). The proliferated cells become associated with the tips of these branches as they advance, but maintain their connections with the body wall until 156 h (Fig. 32, 33). Gradually, the cells from the proliferations spread over the surface of the tracheal commissure (Fig. 25, 38, 56). At later stages, they are very difficult to see because they so closely resemble cells of the tracheal epithelium (Fig. 25, 56).

We believe these cellular proliferations to constitute the prothoracic glands. We have no idea how far they spread over tracheae 1, 2 and 9 (Rempel and Church 1972, Fig. 6, 9, 17), since, even in mature larvae of other beetles, such glands are difficult to trace (Svrivastava 1959). Additionally, the area between the subesophageal-prothoracic interganglionic connectives is eventually occupied by a complex array of tracheal branches (Fig. 56). This also causes difficulties in distinguishing between glandular and tracheal tissues.

## DISCUSSION

### Central and Stomatogastric Nervous Systems

Embryogenesis of the brain, lateral nerve cords and stomatogastric nervous system in *Lytta viridana* has been described very briefly because the sequence of events is so similar to that occurring in *Tenebrio molitor* L. (Ullmann, 1967) and *Sitophilus* [= *Calendra*] *oryzae* (L.) (Coleoptera, Curculionidae) (Tiegs and Murray 1938).

*The median strand* – Authors agree generally about the origin of this system, and the description we have presented outlines the usual pattern. The median strand arises from ectodermal cells along the mid-ventral line of an embryo in a region extending from behind the intercalary segment to the end of the tenth abdominal segment. Early in its development, two types of cells are recognized. In intrasegmental regions, cells of the median strand resemble those of the body wall ectoderm; in intersegmental regions, they assume the appearance of neuroblasts. These latter cells divide teloblastically, like typical neuroblasts, and in fact, seem to be neuroblasts. Nonetheless, we prefer to use the word "clump" for groups of these cells, as did Springer (1967) and Springer and Rutschky (1969). The forward shift of each clump of the median strand from an intersegmental to an intrasegmental position is in agreement with descriptions of this process for other insects (Springer 1967; Springer and Rutschky 1969).

General agreement about development of the median strand gives way to disagreement and controversy about fate and role of the components of this system (Edwards 1969; Anderson 1972a and b and 1973). Details are provided below.

*Fate and role of the clumps of the median strand* – Ullmann (1967) and Springer and Rutschky (1969) summarized information presented by earlier workers about this topic. It was claimed by Ullmann and others that clumps in embryos of *S. oryzae* and *T. molitor* contribute to development of the definitive ganglia, whereas in the insects studied by Springer and Rutschky (various hemipterans, orthopterans, beetles, moths and dipterans), the clumps disappear after katatrepsis. In embryos of *L. viridana*, the clumps are present from their first appearance (56 h) until after hatching (±250 h). We agree with Ullmann (1967) that these cells probably act as ganglion cells because they develop axons (Fig. 11, 19, 47).

Although, for most insects studied, the clump cells seem to be involved with development of the nervous system, Miyakawa (1974) reports that in embryos of *S. griseipennis*, the interganglionic portions of the median cord of the thoracic segments develop into furcae, and thus do not have a nervous function.

*Clumps of the median strand and segmentation of the insect head.*– Because the clumps are intersegmental in all post-oral segments, we assume that in ancestral hexapods they were present also in those segments that arise post-orally but which, in more highly evolved stocks, become pre-oral. If one could recognize the clumps in heads of extant insects, one would have additional evidence for deducing the number of segments involved therein. (See Malzacher 1968; Scholl 1969; Rempel and Church 1971; and Rempel 1975 for comprehensive discussions of head segmentation). Although it is tempting to suggest that the stomatogastric nervous system with its three ganglia (frontal, hypocerebral, and ventricular) is the forward continuation of the median strand, and that the ganglia represent respectively the clumps of the preantennal (labral), antennal, and tritocerebral segments, this is probably not so, for the following reasons: As cephalization occurred, the floors of these segments supposedly contributed to the floor of the stomodaeum. However, each post-oral clump is situated behind the posterior cross commissure of its ganglion. How then could the clump of, for instance, the tritocerebral segment, get onto the roof of the stomodaeum to form the ventricular ganglion while its commissure remained post-oral? It seems developmentally impossible. Thus, it also

seems impossible that these ganglia are the homologues of clumps of the median strand. Probably in extant insects, the segments in question are without a median strand and without clumps, and this is probably the result of atrophy occurring in the extinct ancestral stock.

*Role of the intraganglionic portions of the median strand.* – Springer (1967) and Springer and Rutschky (1969) showed that cells in this region do not become functional ganglion cells, and this seems to be generally accepted. However, authors disagree about what these cells do. Ullmann (1967) claimed that those near the periphery contribute to formation of the perilemma in dorsal portions of the ganglia. On the other hand, Miyakawa (1974) reported that, in *S. griseipennis* embryos, the perilemma over most of each ganglion seemed to arise from modified outer ganglion cells. Our observations for *L. viridana* embryos support the conclusion of Miyakawa.

Cells of the intraganglionic portions of the median strand are involved in production of glial cells. We believe that glial elements associated with axons of the interganglionic connectives also originate from the median strand. We conclude, therefore, that the principal role of the median cord is to form glial cells associated with nerve fibres of the lateral nerve cords.

More specifically, in embryos of *L. viridana* at 104 h, some median strand cells move laterally between neuropile and innermost ganglion cells to form an inner sheath of glial cells (Fig. 20, 43, gll. c), a process very similar to that occurring in embryos of *S. griseipennis* (Miyakawa 1974). We disagree with Springer and Rutschky (1969) who claimed that the inner sheath develops from the innermost ganglion cells.

*Glial cells.* – Three of the four types of glial cells described by Wigglesworth (1972) from specimens of *Rhodnius prolixus* Stål (Heteroptera) are evident in larvae of *L. viridana* that are ready to hatch (prolarvae). These cells are illustrated in Fig. 44: type i (perineurium); type ii (cells scattered among ganglion cells); and type iv (neuropile sheath). Type iii cells having giant nuclei are not present, although some type iv cells have quite large nuclei. All three types of glial cells are also evident in ganglia of the stomatogastric nervous system.

## Endocrine System

This includes the corpora cardiaca, corpora allata, and prothoracic glands. Each of these paired glands is discussed below.

*Corpora cardiaca.* – Embryogenesis of these glands has been studied by a number of workers, notably Weismann (1926, in *C. morosus*), Roonwal (1937, in *Locusta migratoria* (L.) (Orthoptera)), Pflugfelder (1937, in *C. morosus*), and Dorn (1972, and 1975a, in *O. fasciatus*). All agree that ontogenetically, these glands originate with the hypocerebral ganglion, by cell migration from the roof of the stomodaeum.

Dorn (1975a) followed embryogenesis of the corpora cardiaca in eggs of *O. fasciatus*, using the transmission electron microscope. In these insects, the glands appear at 56 h, and begin to differentiate into glandular and glial components at 96 h. The glandular cells assume a spherical distribution about a lumen (his Fig. 4 and 8) into which grow cell projections, probably axons of the *nervi corporis cardiaci*. This occurs when the glands attach to the aorta. Evidence of protein synthesis appears at 96 h, and by 111 h, neurosecretory granules are evident. During hatching (at 124 h) the cells of the glands appear to be secretory.

Secretory cells in the cardiaca of embryos of *L. viridana* are probably homologous with the "instrinsic secretory cells" described by Schoonveld (1970) in the cardiaca of adult specimens of *Leptinotarsa decemlineata* Say (Coleoptera, Chrysomelidae).

Phylogenetically, Hanström (1942) assumed the corpora cardiaca to have evolved from a stomodaeal ganglion. Because these glands occur in all apterygote insects which have been examined for them, and because the corpora allata do not, Novák (1975) assumed that the former glands are evolutionarily older than the latter glands.

*Corpora allata.* – In embryos of different taxa of insects, these glands seem to originate from different germ layers, and in different positions. For example, in embryos of *L. viridana, O. fasciatus* (Dorn 1972), and *S. griseipennis* (Miyakawa 1974), they arise as ectodermal invaginations at the anterior base of each maxilla. On the other hand, in *L. migratoria* (Roonwal 1937) and *C. morosus* embryos (Pflugfelder 1937), the glands arise as paired, ectodermal invaginations between the mandibular and maxillary segments. And, in embryos of *S. oryzae*, they originate from mesoderm of the antennal coelomic sacs (Tiegs and Murray 1938). According to Pflugfelder (1937), some authors have even reported corpora allata as being of endodermal origin. Probably some of these observations are incorrect. Certainly the question of ontogenetic origin of these glands should be investigated using a wide taxonomic spectrum of pterygote insects and a diversity of approaches.

The ultrastructure and function of the developing corpora allata of *O. fasciatus* embryos have been studied by Dorn (1975 b) who showed that high titers of juvenile hormone present just before hatching are probably the result of activity of these glands.

*Prothoracic glands.* – For Coleoptera, Srivastava (1959) described the prothoracic glands of larvae of 15 species (none were meloids). These glands occur in the head, cervical region and prothorax as thin cords or sheets of cells closely associated with one or both of two large tracheae extending from the prothoracic spiracles into the head. Embryogenesis of the prothoracic glands was previously unknown for Coleoptera, and has been little studied in any insect species.

Differences of opinion among authors suggest i) that the prothoracic glands of different insects are not homologous, or ii) that some accounts of their origin are in error, or iii) that some tissues referred to as prothoracic glands are some other structure. We cannot resolve the problem, but we review the different viewpoints, below.

According to Gilbert and King (1973), Toyama (1902) identified the prothoracic glands in embryos of *Bombyx mori* L. (Lepidoptera) as epithelial invaginations of the labial segment of the head. A similar origin was postulated for the glands of embryos of *Dysdercus cingulatus* (Fab.) (Heteroptera) by Wells (1954), and for those of *O. fasciatus* embryos by Dorn (1972). In embryos of *Schistocerca gregaria* (Forskål) (Orthoptera), the prothoracic glands invaginate before katatrepsis from lateral ectodermal regions between the maxillary and labial segments (Micciarelli and Sbrenna 1972). Novák (1975) suggested that the prothoracic glands of most pterygote insects originate from the ventral margin of the prothoracic segment, basing his conclusion on their innervation from the prothorax, and on their supposed homology with the cephalic nephridia of apterygote insects. The proposed labial-prothoracic origin for these glands in *L. viridana* embryos, if proved, would support Novák's conclusion.

We at first thought that the labial diverticula (Fig. 19, lb. div), not the intersegmental proliferations suggested here, might be the progenitors of the prothoracic glands, because these diverticula originate from the labial segment, as do the glands of some of the insects named above. The diverticula grow caudad under the suboesophageal ganglion where they bend abruptly upward to end in the labial-prothoracic region. Ullmann (1967) detailed evidence to suggest that these diverticula develop into "maxillary glands". We have followed developmentally the "glands" of *L. viridana* embryos to similar but very indistinctly developed structures in prolarvae of this species.

Publications also present conflicting evidence concerning the function of embryonic prothoracic glands (see discussions and refs. in Dorn 1972; and Micciarelli and Sbrenna (1972)). Dorn (1972) noted that the glands of *O. fasciatus* showed three cycles of activity (as did the neurosecretory cells and corpora cardiaca) that correlated well with secretion of three prehatch cuticles. A similar correlation was noted by Micciarelli and Sbrenna (1972) in the two moults of *S. gregaria* embryos. However, these authors showed that isolated embryonic abdomens, lacking these glands, were also capable of secreting two cuticles and concluded that

embryonic apolyses are not under control of the prothoracic glands. Since much recent evidence suggests that ecdysone can be synthesized in organs other than the prothoracic glands (Nakanishi, *et al.* 1972; Romer, *et al.* 1974; Hsiao, *et al.* 1975), action of this hormone in embryonic moults has still not been ruled out.

Embryos of *L. viridana* produce a single, delicate embryonic cuticle between 120 and 132 h, shortly after katatrepsis, about the time that secretory cells become evident in the corpora cardiaca. However, there is no obvious change at this time in cells of the corpora allata or prothoracic glands. Neither is any change noted in these cells at 168 to 180 h, when deposition of larvae cuticle begins. Thus, we have no positive evidence of endocrine function in embryos of *L. viridana*.

Writing the above discussion on the origin and function of embryonic insect endocrines was frustrating because of the conflicting results presented in the literature. We do not believe that structures as fundamental to insect development as the corpora allata and prothoracic glands can have so many different ontogenetic origins. Diversity in site of origin implies multiple independent origin during insect evolution. This conflicts with the proven similarity in biochemical function of these glands in representative insects of most orders (Gilbert and King 1973; Slama, *et al.* 1974; Novák 1975). What is required to resolve the conflict are detailed comparative embryological studies of the most critical kind using all methods available. Dorn's (1972, 1975 a, b) studies in which conventional, ultrastructural and experimental methods are combined, provide a start in the right direction. It would also help if embryological studies the quality of Dorn's were carried out on individuals of species for which experimental proof of gland function exists.

## ACKNOWLEDGEMENTS

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## ABBREVIATIONS

| | | | |
|---|---|---|---|
| abd. ggl | abdominal ganglia | mdgt | midgut |
| ant | antenna | mes | mesoderm |
| ant. s. o | antennal sense organ | m. n. c | median nerve cord |
| a. tent | anterior tentorial arm | mx | maxilla |
| bd. w | body wall | mx. ggl | maxillary ganglion |
| brn | brain | nbl | neuroblast |
| com | commissure | ng. l | neurogene layer |
| crp. all | corpus allatum | npl | neuropile |
| crp. crd | corpus cardiacum | nr. lml | neural lamella |
| cyt. std | cytoplasmic strand | nv | nerve |
| deutc | deutocerebrum | op. c | optic cup |
| dg. l | dermatogene layer | op. l | optic lobe |
| ect | ectoderm | prn | perineurium |
| ent. r | enteron rudiment | protc | protocerebrum |
| frt. ggl | frontal ganglion | prs. intr | pars intercerebralis |
| ggl. c | ganglion cell | p. tent | posterior tentorial arm |
| gll. c | glial cell | rct. nv | recurrent nerve |
| haem | haemocytes | s | secretory cells of corpora cardiaca |
| hyp. ggl | hypocerebral ganglion | sb. ggl | subesophageal ganglion |
| int. cn | interganglionic connectives | spl. m | splanchnic mesoderm |
| intc. ect | intercalary ectoderm | stmg. n. s | stomatogastric nervous system |
| intc. seg | intercalary segment | stom | stomodaeum |
| lb | labium | stom. rf | roof of stomodaeum |
| lb. div | labial diverticulum | sub. b | subesophageal body |
| lb. ggl | labial ganglion | tr. com | tritocerebral commissure |
| lm | labrum | tent | tentorium |
| l. n. c | lateral nerve cord | thr. ggl | thoracic ganglia |
| m. c. c | median strand clump | trch | trachea |
| md | mandible | tritc | tritocerebrum |
| md. flx. ap | mandibular flexor apodeme | vnt. ggl | ventricular ganglion |
| md. ggl | mandibular ganglion | yk | yolk |

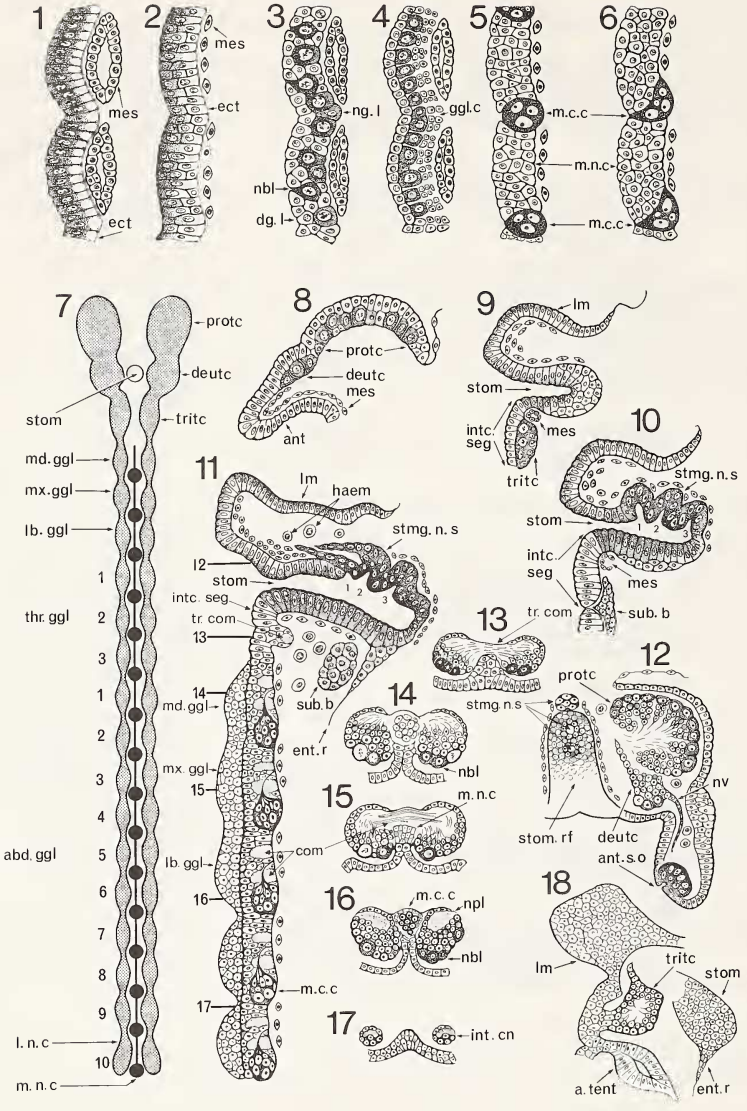



Fig. 1. Body wall and coelomic sacs at 50 h, parasagittal section. Fig. 2. Body wall at 50 h, median sagittal section. Fig. 3. Same, at 56 h, parasagittal section, showing dermatogene (dg. l) and neurogene (ng. l) layers, the latter with neuroblasts (nbl). Fig. 4. Same, at 60 h, showing formation of pre ganglion and ganglion cells (ggl. c). Fig. 5. Same, median sagittal section, showing "clumps" of median strand cells (m.c.c). Fig. 6. Same, at 64 h, showing forward shift of median strand clump. Fig. 7. Diagram of central nervous system, showing cephalic ganglia, lateral nerve cords (l.n.c) and median nerve strand (m.n.c). Fig. 8. Parasagittal section through protocephalic lobe and antenna (ant) at 56 h, showing formation of protocerebral (protc) and deutocerebral (deutc) neuroblasts. Fig. 9. Same, through stomodaeum, showing formation of tritocerebral (tritc) neuroblasts from intercalary ectoderm (intc. seg). Fig. 10. Median sagittal section through stomodaeum at 64 h, showing formation of stomatogastric nervous system (stmg. n.s). Fig. 11. Same, at 88 h, showing median strand clumps (m.c.c). Fig. 12-17. Transverse sections through developing nerve cord at 88 h, taken at points indicated by lines in Fig. 11: 12, Through antenna and stomodaeum, showing developing ganglion cells, stomatogastric nervous system, (stmg. n.s) and antennal sense organ (ant. s.o); 13, Through tritocerebral ganglion; 14, Through mandibular ganglion; 15, Through posterior commissure of maxillary ganglion; 16, Through median strand "clump" (m.c.c) of labial ganglion; 17, Through prothoracic-mesothoracic intersegmental region and inter ganglionic connectives (int. cn). Fig. 18. Parasagittal section through tritocerebral ganglion (tritc) and anterior tentorial arm (a. tent).

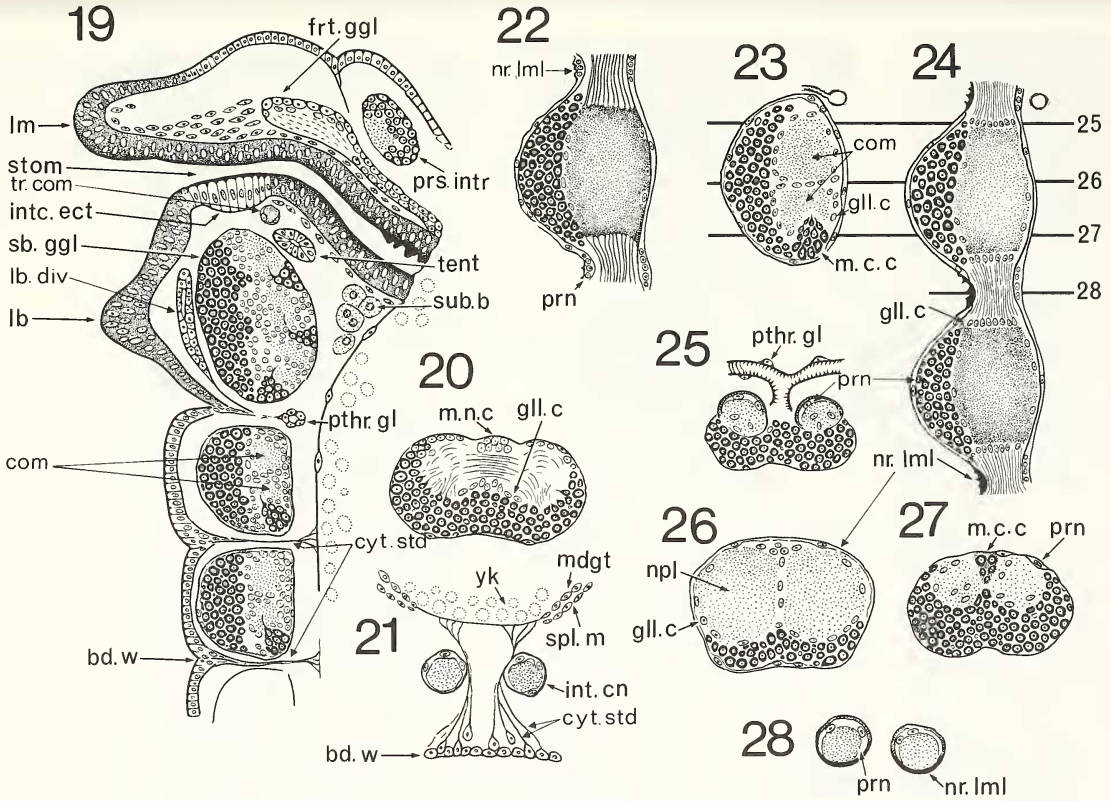



Fig. 19. Median sagittal section through cephalic region of 120 h embryo, showing prothoracic gland (pthr. gl). Fig. 20. Transverse section through subesophageal ganglion of 120 h embryo. Fig. 21. Same, through prothoracic-mesothoracic intersegmental region, showing developing interganglionic connectives (int. cn) and cytoplasmic strands (cyt. std). Fig. 22. Parasagittal section through an abdominal ganglion of an 132 h embryo. Fig. 23. Median sagittal section through an abdominal ganglion of an 180 h embryo, showing glial cells (gll. c), cross commissures (com), and median strand clump (m. c. c). Fig. 24. Parasagittal section through two abdominal ganglia and interganglionic connective of an 180 h embryo, showing perineurium (prn), neural lamella (nr. lml) and glial cells (gll. c). Fig. 25-28. Transverse sections through ventral nerve cord of thorax of 180 h embryo taken approximately at points shown by lines in Fig. 24: Fig. 25, through interganglionic connectives linking subesophageal and prothoracic ganglia, note prothoracic gland cells (pthr. gl); Fig. 26, through prothoracic ganglion, showing neuropile (npl) and glial cells (gll. c); Fig. 27, through posterior region of prothoracic ganglion, showing median strand clump (m. c. c); Fig. 28, through prothoracic-mesothoracic interganglionic connectives, showing their inner perineurium (pnr) and outer neural lamella (nr. lml).

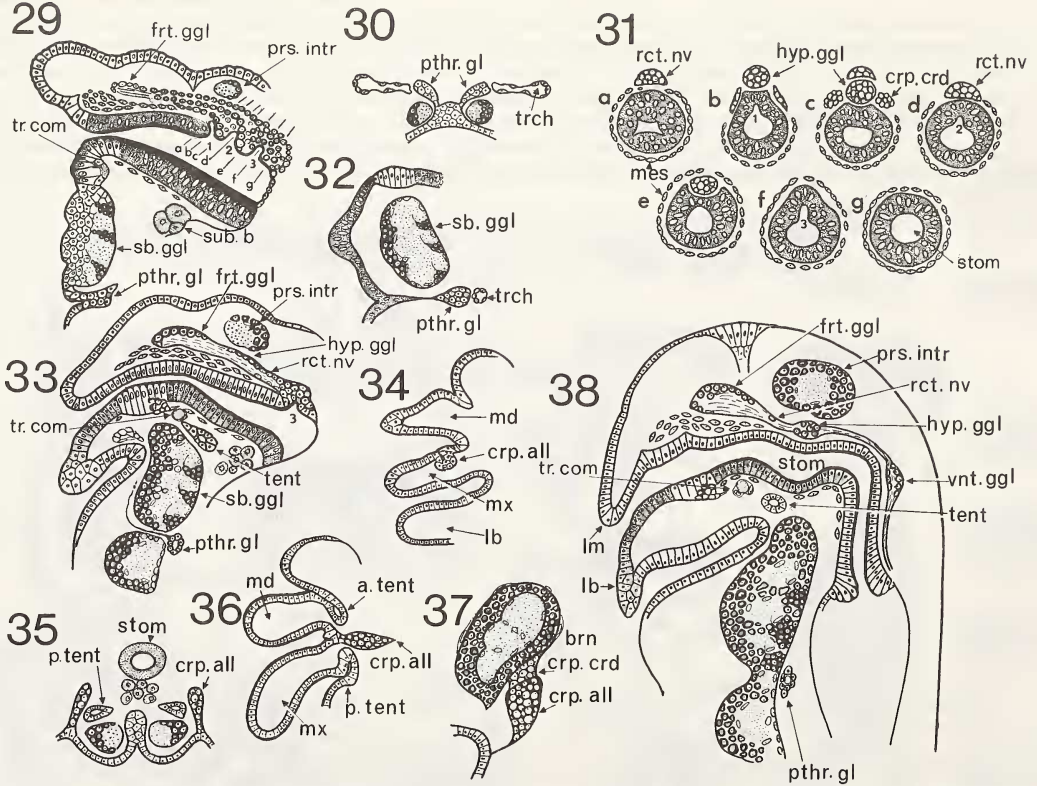



Fig. 29. Median sagittal section through stomodaeum at 104 h, showing developing stomatogastric nervous system. Fig. 30. Transverse section through labial-prothoracic intersegmental region at 104 h, showing origin of prothoracic glands (pthr. gl). Fig. 31. Transverse sections through stomodaeum (stom) of 104 h embryo taken at points indicated by lines in Fig. 29. Fig. 32. Median sagittal section through gnathal region of 120 h embryo. Fig. 33. Same, through stomodaeum of 132 h embryo, showing developing prothoracic glands (pthr. gl). Fig. 34. Parasagittal section through gnathal appendages of 88 h embryo, showing anlage of corpus allatum (crp. all). Fig. 35. Transverse section through mandibular-maxillary intersegmental region of 104 h embryo, showing developing corpora allata (crp. all). Fig. 36. Parasagittal section through gnathal appendages of 104 h embryo, showing dorsal growth of corpus allatum (crp. all) between anterior (a. tent) and posterior (p. tent) tentorial arms. Fig. 37. Parasagittal section of 180 h embryo, showing brain (brn), corpus cardiacum (crp. card) and corpus allatum (crp. all). Fig. 38. Median sagittal section through head of 216 h embryo, showing complete stomatogastric nervous system and transverse profile of prothoracic gland (pthr. gl).

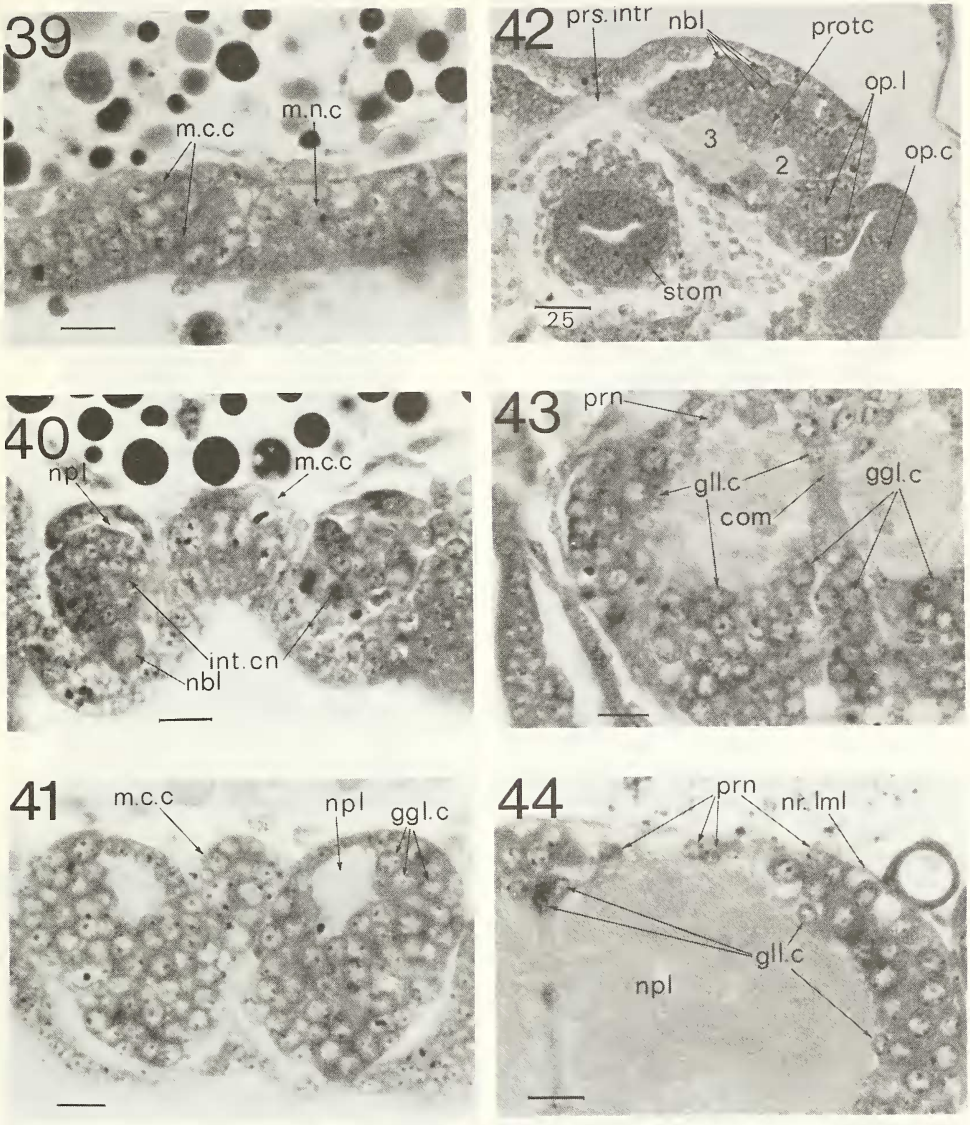
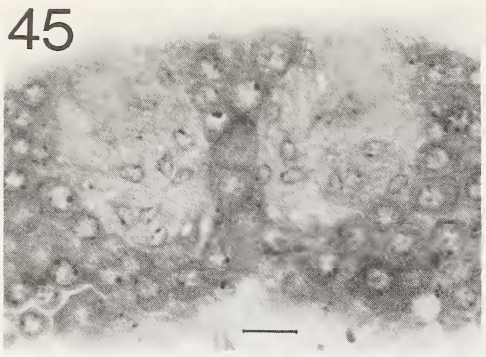
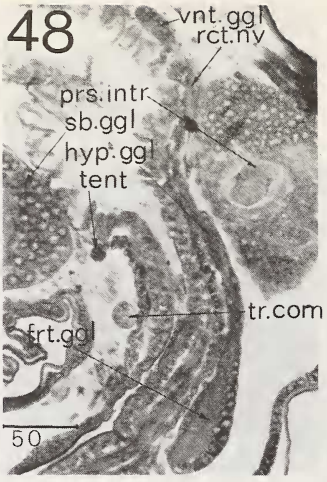
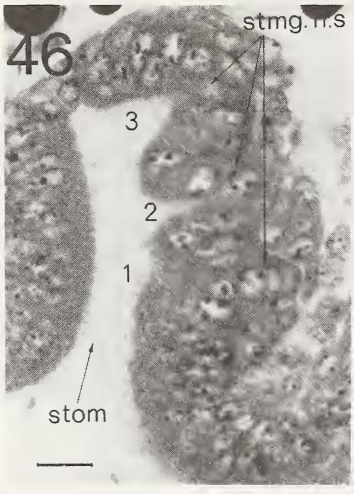
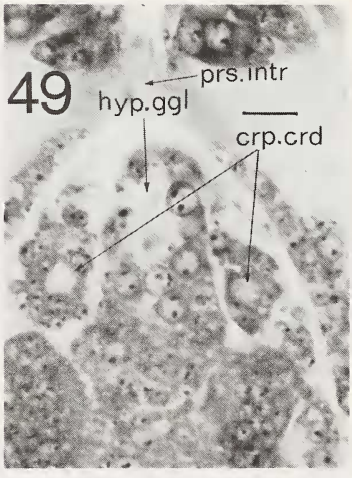


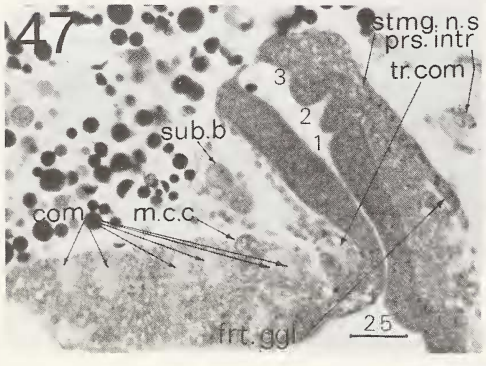

Fig. 39-56. Photomicrographs, scale 10 µm except where indicated. Fig. 39. Median sagittal section of 72 h embryo, showing forward shift of maxillary median strand clump (m. c. c). Fig. 40. Transverse section through maxillary median strand clump (m. c. c) and interganglionic connectives (int. cn) of 72 h embryo, showing neuroblast (nbl) and developing neuropile (npl). Fig. 41. Same, of 96 h embryo through median strand clump (m. c. c) of labial ganglion. Fig. 42. Frontal section through head of 96 h embryo, showing three lobes of protocerebrum (protc), lobe 1 (op. l) developing as an invagination. Note optic cup (op. c). Fig. 43. Transverse section through labial commissure (com) of subesophageal ganglion of 120 h embryo. Note developing glial cells (gll. c) and perineurium (prn). Fig. 44. Same, through subesophageal ganglion of 264 h embryo, showing glial cells (gll. c), perineurium (prn) and neural lamella (nr. lml).



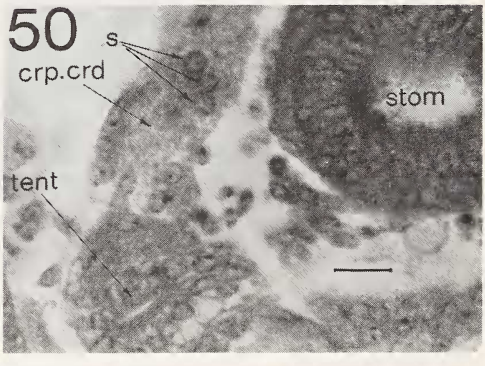
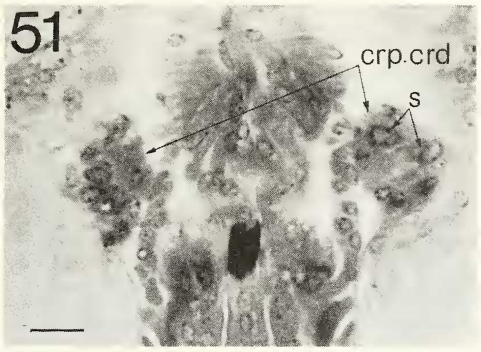
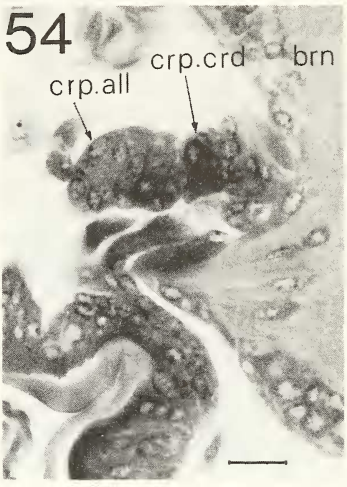
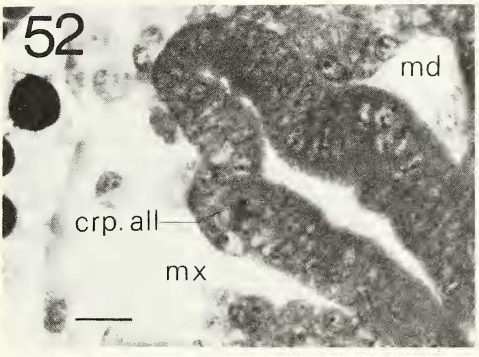
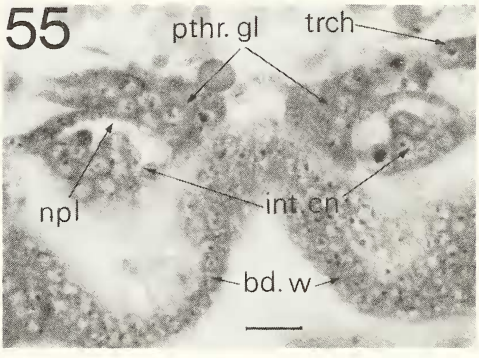



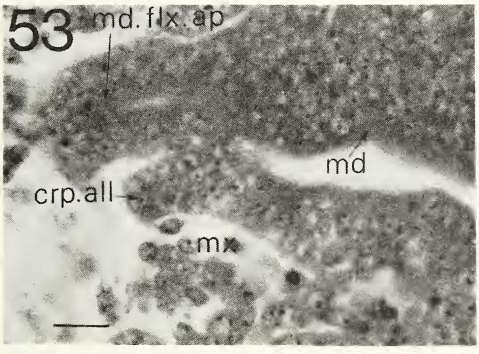

Fig. 45. Transverse section through anterior ends of subesophageal-prothoracic interganglionic connectives of 264 h embryo, showing glial cells in neuropile. Fig. 46. Median sagittal section through stomodaeum (stom) of 72 h embryo, showing evaginations of stomatogastric nervous system (stmg. n. s). Fig. 47. Same, of 96 h embryo, showing tritocerebral commissure (tr. com) and those of subesophageal ganglion (com). Note also the mandibular median strand clump (m. c. c). Fig. 48. Same, of 264 h embryo, showing frontal (frt. ggl), hypocerebral (hyp. ggl), and ventricular ganglia (vnt. ggl). Fig. 49. Transverse section through 96 h embryo, showing corpora cardiaca (crp. crd) and hypocerebral ganglion (hyp. ggl). Fig. 50. Same, through 120 h embryo. Note secretory cells (s) in corpus cardiacum (crp. crd).



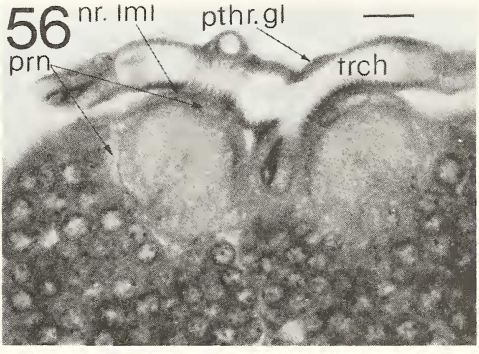




Fig. 51. Transverse section through corpora cardiaca (crp. crd) of 264 h embryo. Fig. 52. Parasagittal section through base of maxilla (mx) of 88 h embryo, showing invaginating corpus allatum (crp. all). Fig. 53. Same, 96 h. Fig. 54. Same, through corpus cardiacum - corpus allatum complex of 252 h embryo. Note delicate strand extending from apex of corpus allatum (crp. all). Fig. 55. Transverse section through labial-prothoracic intersegmental region at 96 h, showing origin of prothoracic glands (pthr. gl). Fig. 56. Same, 264 h.